

# SACCOCOMA: A BENTHIC CRINOID FROM THE JURASSIC SOLNHOFEN LIMESTONE, GERMANY

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**ABSTRACT.** *Saccocoma* is the most numerous macrofossil in the Solnhofen Limestone but its study has been relatively neglected. Functional interpretations of the morphology and mode of life have been based on Jaekel's definitive paper (1892) in which the lifestyle of *Saccocoma* was considered to be pelagic. However, new morphological interpretations suggest that *Saccocoma* may have been benthic. This conflicts with the conventional interpretation of the Solnhofen environments which proposes that adverse conditions precluded colonization by benthos.

*SACCOCOMA* was first illustrated by Bajer in 1730 (*vide* Bather 1924), and referred to by Goldfuss (1829), who assigned it to the order Comatulida. It was described and named by Agassiz in 1835. Quenstedt (1852) placed the saccocomids in the Asteroida. The Saccocomidae was established by d'Orbigny (1852), but he did not place the family in a phylogenetic context. Zittel (1879) redescribed the material of Goldfuss (1829), emphasizing the similarities between the saccocomids and crinoids rather than ophiuroids. The most detailed description of *Saccocoma* was given in Jaekel (1892). This exhaustive work has formed the basis of all current theories of the functional morphology and mode of life of *Saccocoma*. Two main species were described: *S. tenella* and the juvenile equivalent *S. pectinata* (Jaekel 1892). Walther (1904) included *Saccocoma* in his review of the fauna of the Solnhofen Plattenkalk and described a new species, *S. schwertschlagerei*. Recent work has involved the identification and revision of the species belonging to *Saccocoma*. Key specific descriptions were given by Sieverts-Doreck (1955), Verniory (1960 [*S. tenella*], 1961 [*S. quenstedti*], 1962), Hess (1972 [*S. schattenbergi* and *S. subornata*]) and Manni and Nicosia (1984 [*S. vernioryi*]). Manni and Nicosia (1985) regarded *S. schwertschlagerei* as a junior synonym of *S. tenella*.

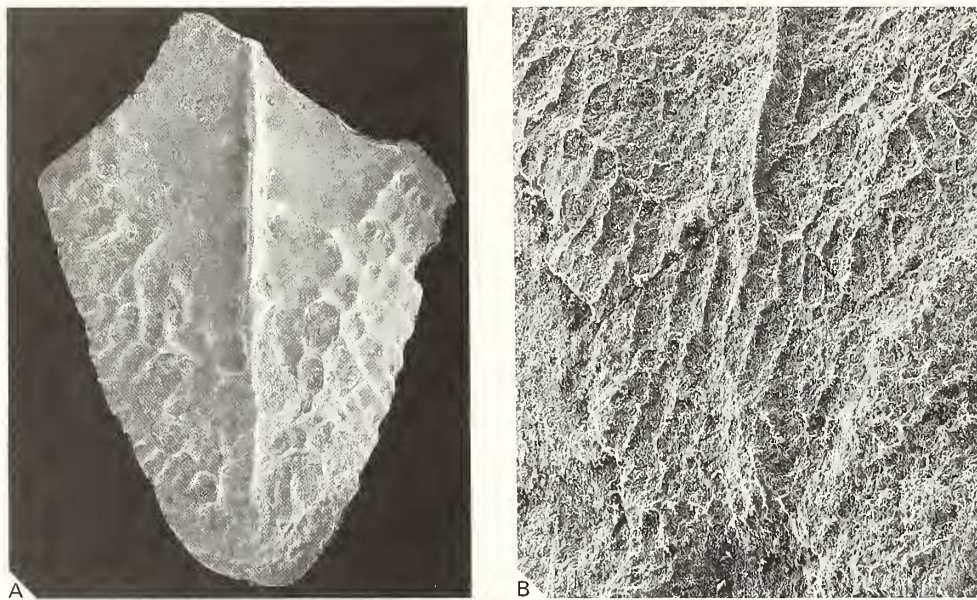
*Saccocoma* is the most numerous macrofossil in the Solnhofen lithographic limestones. This fossil Lagerstätte (Seilacher *et al.* 1985), famous for the preservation of medusae and *Archaeopteryx* with feathers, was deposited in the late Jurassic. The most fossiliferous unit of the Lagerstätte is the Upper Solnhofen Plattenkalk which was formed in the Early Tithonian ( $ti_{2b}$ ) in the area extending from Langenthalheim to Kelheim. *S. tenella* (including its juvenile stage *S. pectinata*) are most abundant in the Eichstätt quarries where slabs covered with the crinoid occur. The abundance of *Saccocoma* decreases in a south-westerly direction towards the Solnhofen quarries where specimens are relatively rare.

*Saccocoma tenella* is also common in the Upper Kimmeridgian of Kimmeridge Bay (Arkell 1947) where, unlike in the Solnhofen Limestone, preservation is poor. Only isolated ossicles are found and these are rarely complete. *S. tenella* also occurs in the Kimmeridgian at Talloires near Lake Annecy in the Haute-Savoie district of France (Verniory 1960, 1962). *S. vernioryi* is reported from the Tithonian of Marche, Italy (Manni and Nicosia 1985). *S. tenella* and *S. quenstedti* occur in the Upper Oxfordian of Sisteron, Provence, France, the Malm 6 ( $\equiv$  Middle Kimmeridgian ( $ki_2$ )) of Württemberg, Germany (Verniory 1961, 1962), and the late Jurassic of the North American Atlantic seaboard (Hess 1972). *S. schattenbergi* comes from the Middle to Upper Oxfordian at Faucigny, Haute-Savoie, France (Verniory 1962), and the late Jurassic of the American Atlantic seaboard (Hess 1972). *S. subornata* occurs in the 'Weissjura Gamma' (Lower Kimmeridgian) of Southern Germany and the late Jurassic of the North American Atlantic seaboard (Hess 1972).

## GENERAL MORPHOLOGY

The calyx of *Saccocoma* is bowl shaped with a convex base. It is composed of one main circlet of five large radial plates, five very small basals and a minute centrale. These enclose a large, undivided cup-shaped body cavity. The radial plates have a convex surface and taper aborally. They are connected at their lateral margins by a prominent zig-zag suture. The articular facet is medially placed at the position of the oral margin. The tegmen is not preserved.

The radials form the main part of the calyx. Their inner surface is smooth but the exterior is covered with a complicated reticulate sculpture (Text-fig. 1). The network of anastomosing ridges



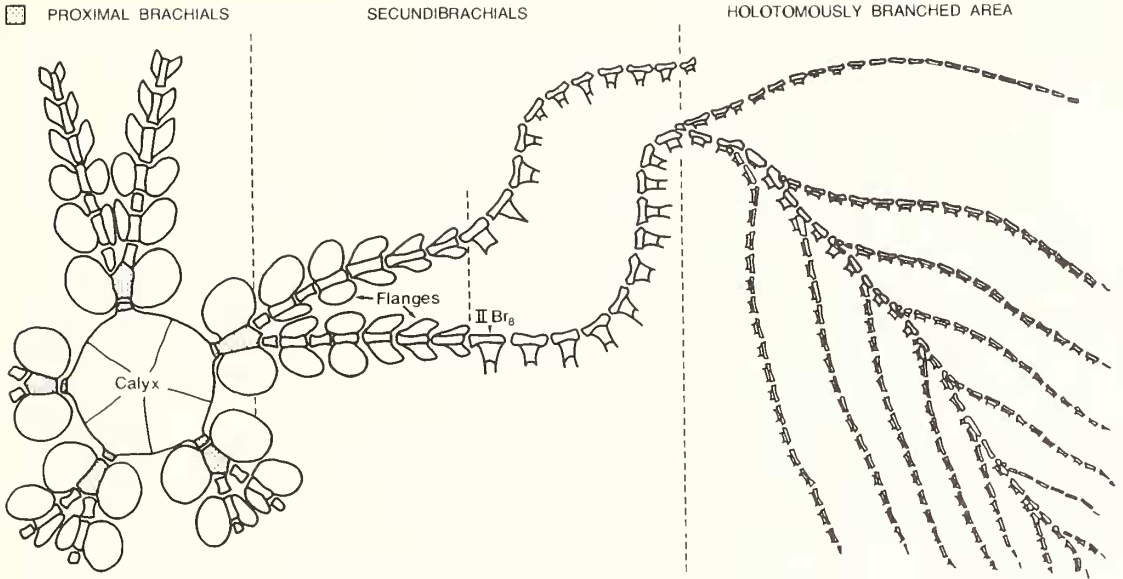
TEXT-FIG. 1. A, reticulate ornament on the radial plates of *Saccocoma tenella*, Kimmeridge Clay, Dorset;  $\times 125$ . B, detail of anastomosing ridges;  $\times 1250$ .

is more irregular in the centre of the plate, becoming more organized towards the plate margins where the ridges are broadly parallel and perpendicular to plate sutures. The lateral edges are denticulate and the suture between two radials is formed by the interdigitation of the ridges. The projecting ridges are inserted between the neighbouring ridges, thus forming a zig-zag suture. The plates are extremely thin and feather out towards the lateral margins so that only the anastomosing network of the outer ridges remains at the plate edges.

The articular facet is positioned at the centre of the ventral margin of the radial plate. It is small, horizontal and lacks any distinct type of articulation.

The arms are uniserial. They dichotomize on the second brachial and distally branch holotomously. The arms can therefore be divided into three parts (Text-fig. 2); the proximal part, the secundiarm, and the holotomously branched region. The proximal part is an atomous section of the arm consisting of two brachials only, the first primibrach  $\text{IBr}_1$  and the primaxil  $\text{IBr}_2$ .

Primibrach  $\text{IBr}_1$  is a simple, small, cylindrical ossicle which tapers distally. The ventral surface is characterized by two distal grooves which diverge distally. Primaxil  $\text{IBr}_2$  is ornamented with large wing-like flanges which are attached to the lateral margins of the brachial. These wings are concave and smooth dorsally. The secundiarm consists of around seventeen unbranched secundibrachials showing three morphological styles.  $\text{IIBr}_1$  and  $\text{IIBr}_3$  correspond to hypozygal brachials of syzygal



TEXT-FIG. 2. Division of the arm of *Saccocoma* into three parts. Redrawn from Jaekel (1892).

pairs which in other crinoids lack pinnules. Brachials  $IIBr_{1,3}$  are small and unornamented; in contrast,  $IIBr_{2,4-7}$  are ornamented with the paired lateral wing-like expansions seen on the  $IBr_2$  ossicle. Paired processes also occur on  $IIBr_{8-17}$  but they are attached to the lateral margins of the aboral brachial surface and are parallel to each other and rectangular in outline. In the holotomously branched part of the arm ramules are added regularly on alternate sides of every other brachial. Ramule length decreases distally. The brachials are almost identical to the distal secundibrachials except that they are smaller and the lateral processes are reduced.

#### PREVIOUS INTERPRETATIONS OF FUNCTIONAL MORPHOLOGY AND MODE OF LIFE

The most detailed functional interpretation of the morphology of *Saccocoma* was given by Jaekel (1892); he highlighted the delicate nature of the ossicles, particularly the radials, where weight had been reduced to such an extent that only the anastomosing ridges exist at the radial margins. Jaekel interpreted these ridges as structural supports which were necessary in order to compensate for the loss of strength resulting from extreme weight reduction. As the network of ridges occurs on the most distal brachials, he concluded that weight reduction occurred in all ossicles. This weight reduction combined with the absence of a mode of attachment formed the foundation of the pelagic hypothesis.

Jaekel (1892) interpreted the lateral flanges or 'wings' which occur on the  $IBr_2$  and  $IIBr_{2,4-7}$  brachials as supports for a membrane which would expand across this area, thus connecting the lower parts of all arms, as in an octopus. Therefore the function of these 'wings' would be to strengthen parts of the connecting skin. He suggested that the size difference between the adradial 'wings' and the larger abradial 'wings' prevented interference between wings of the same arm during locomotion. Interpolated with these winged brachials are the wingless  $IIBr_1$  and  $IIBr_3$  ossicles. According to Jaekel these ossicles aided mobility, and without them the wings of adjacent brachials would interfere.

The ventrally directed vertical projections which occur from  $IIBr_8$  onwards Jaekel (1892) also interpreted as soft tissue supports, but in this case rather than connecting the arms radially, the

tissue extended along the length of the arm forming a continuous channel within which the tube feet could operate. Without these extensions Jaekel suggested that the activity of the tube feet would have been limited due to the narrowness of the arms. Jaekel cited these structures as further evidence of skeletal lightening.

The calyx is too small to enclose an efficient buoyancy aid, such as a gas bubble or fatty deposit; however, Jaekel (1892) predicted that a buoyancy aid would be unnecessary or only a small aid would be required to offset the minimal weight of the skeleton. Thus he concluded that *Saccocoma* was planktonic, passively driven along with the current, in a similar manner to a jellyfish, with mouth down and arms pendant.

Further to Jaekel's (1892) interpretation, Seilacher *et al.* (1985) suggested that the necrolytic deformation of the arms of the crinoids in the Solnhofen Limestone may be indicative of their flexibility patterns during life. In *Saccocoma* the arms are distally coiled, in contrast to the comatulids in which the proximal part is coiled but the arm tips are conspicuously straight. Thus Seilacher *et al.* concluded that whilst the proximal arm section controls swimming in comatulids, the distal portion was responsible in saccocomids.

Although these functional interpretations are very feasible, they do not represent the only possible scenario. Certain morphological factors have been neglected whilst others require further consideration.

#### ADDITIONAL EVIDENCE OF MODE OF LIFE FROM FUNCTIONAL MORPHOLOGY

##### *Specific gravity*

*Saccocoma* would have been able to stay suspended in mid-water if its density was equal to that of sea water. The crinoid endoskeleton is composed of high-magnesium calcite with a density significantly greater than sea water. As the soft tissue is also denser than sea water it will not compensate for endoskeleton density. Therefore *Saccocoma* must either have been continuously active in order to generate lift economically from its forward motion, or have had a special buoyancy aid. Jaekel (1892) and Seilacher *et al.* (1985) suggested a medusoid mode of life for *Saccocoma*, thus implying the presence of a fluid with a low specific gravity contained within the body tissue. A large volume of low density fluid would be required to offset the excess skeletal and tissue density. In extant medusae, buoyancy fluids only give 1.5 mg lift in sea water for every cubic centimetre of fluid (Denton 1974). This is very little lift and it is only because these animals are unskeltonized that the fluids make the animal buoyant. Even so, jellyfish must swim actively to avoid sinking through the water column. The presence of a fossilized skeleton and the lack of evidence for a large amount of low density material argues against a pelagic mode of life for *Saccocoma*.

##### *Orientation*

Jaekel (1892) suggested that *Saccocoma* floated mouth downwards in the water column. Such an orientation would severely hinder the efficiency with which the crinoid fed. Gislén (cited in Peck 1955) proposed that roveacrinids would have difficulty catching sinking particles if they floated with the mouth downwards. Furthermore, the calcareous dorsal parts would be appreciably heavier than the fleshy ventral parts and would favour a mouth-upwards orientation.

##### *Presence of flanges on IBr<sub>2</sub> and IIBr<sub>2,4-7</sub>*

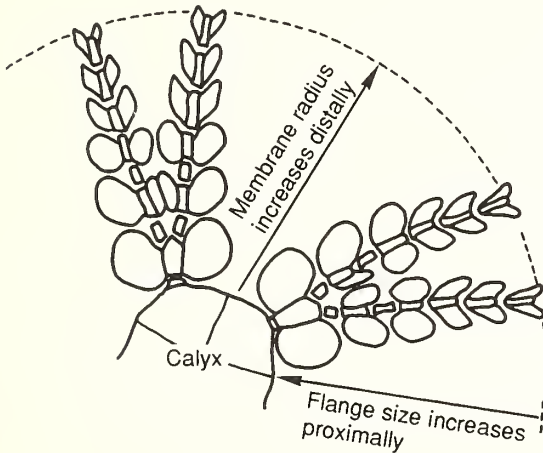
Analysis of disarticulated specimens of *Saccocoma tenella* from the Upper Kimmeridge Clay of Kimmeridge Bay has revealed that these flanged brachials are the most frequently preserved ossicles. The wing-like processes are rarely damaged suggesting that these are the most robust plates in the crinoid skeleton. These heavily calcified ossicles are incongruous with an endoskeleton that

supposedly has been reduced to its minimum weight. The thickness of the radial plates which enclose and protect the visceral mass has been reduced to a minimum; therefore it seems unlikely that an animal would reduce the weight of such vital plates whilst strengthening those which provide support for a supposed connecting membrane.

#### *Presence of a soft tissue membrane*

Although the curved margin of the wing would maximize the area of attachment of the membrane, the wing surface is completely smooth and the curved margins are an unusual shape for membrane attachment. There is no marginal groove or surface ornament to suggest connection to a soft tissue membrane in life. Wing size decreases distally, which is also inconsistent with the support theory. It would be more logical for the area of support required and the radius of the membrane to be directly proportional. However, they are inversely proportional in *Saccocoma* (Text-fig. 3). Rather

TEXT-FIG. 3. Decrease in flange size with an increase in area of the inferred membrane.



than supporting a connecting membrane, for which there is no direct evidence, the brachial wings may have acted as weight distributors performing a function similar to that of a snow-shoe, preventing the arms from sinking into the substrate.

#### *Thinness of the radial plates*

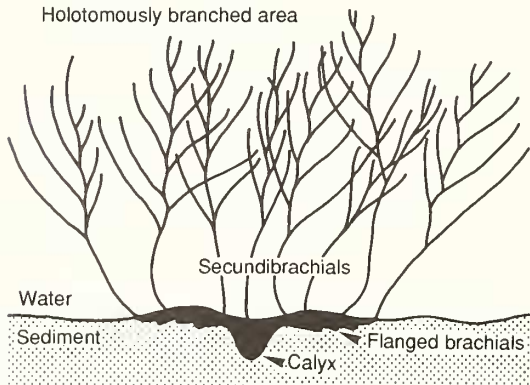
The extreme thinness of the radial plates was cited by Jaekel (1892) as evidence of weight reduction associated with a pelagic lifestyle. However, as the radials enclose the visceral mass, thinning the plates would make the animal extremely vulnerable to predators, particularly if lifestyle was pelagic. If *Saccocoma* lay on the sea floor with the calyx embedded in the sediment, anchored by the reticular sculpture on the radial exterior, the calyx would have been better protected.

#### *Pattern of arm branching*

The saccocomids exhibit an unusual pattern of arm branching. Dichotomy occurs on the second brachial, the arms then remain atomous until approximately IIBr<sub>17</sub>, after which they branch holotomously. Essentially, *Saccocoma* has ten simple arms which feather distally. This arm branching pattern may be related to a unique harvesting mechanism. Cowen (1981) stated that arm branching patterns in crinoids are usually related to harvesting style in different environments. If *Saccocoma* fed passively by gravitational settling of particles the feathered arm sections could form an enclosed collecting bowl and thus an effective feeding net.

PROPOSED MODE OF LIFE FOR *SACCOCOMA*

The mode of life proposed for *Saccocoma* differs fundamentally from the conventional theory in that the general lifestyle is taken to be benthic. Evidence for a benthic mode of life is primarily based on the specific gravity of *Saccocoma* and the absence of a plausible buoyancy or swimming mechanism. Therefore it is proposed that *Saccocoma* lay unattached on the sea floor with the calyx embedded in the sediment and the oral surface close to the sediment/water interface (Text-fig. 4).



TEXT-FIG. 4. Proposed living position of *Saccocoma*.

The proximal parts of the arms lay on the sediment surface and were stabilized by the lateral flanges which distributed the weight and prevented the animal from sinking. They would also provide leverage for elevating the distal, feeding parts of the arms. With the calyx anchored in the substratum, the mouth orientated upwards and the flanged proximal arms arranged radially around the calyx immobilizing the crinoid, the distal section of the arms was free to fulfil the food-gathering functions.

A 'collecting-bowl' feeding posture is postulated for the saccocomids. In the region IIBr<sub>8</sub> to IIBr<sub>17</sub> (between the first parallel-flanged brachial and the most distal secundibrachial before the holotomously branched area), the arms arched upwards. By extending the ramuli outwards, an effective feeding net was formed. Due to the flexibility of the arms, there was the facility for rheophilic feeding when a slight current was present. Under such circumstances the arms could have orientated themselves with the aboral arm surface facing down current, as observed by Meyer (1973) in living comatulids.

The extreme flexibility of the arms, indicated by the extent to which they could coil without rupture, suggests that the crinoid may have been mobile. *Saccocoma* was probably able to crawl across the substrate, aided by extension and contraction of the arms in a similar manner to living comatulids (Shaw and Fontaine 1990). The extended ramuli in the holotomously branched area would produce a large surface area to 'push off' the substrate and, as the arm lifted away from the substrate flattening the ramules against the main arm axis, would minimize drag and thus increase crawling efficiency.

It is also likely that saccocomids had the ability to swim. However, due to high specific gravity, the large amount of energy required to generate lift presumably inhibited spontaneous swimming. Therefore, swimming may have been elicited by current action which lifted the crinoid from the substrate, or, in extreme cases, may have been used as an escape mechanism.

## LIMITATIONS TO PROPOSED BENTHIC MODE OF LIFE

A limiting factor to the proposed lifestyle is the feeding mechanism. The theory proposes that saccocomids normally formed a 'collecting bowl' with which they captured food by gravitational settling of particles. Such rheophobic feeding is extremely rare in living crinoids. Meyer (1973)

stated that deep-sea species of comatulids and stalked crinoids may be rheophobic, although the collecting bowl is only a temporary feeding method exploited when currents are slack.

Although the benthic theory explains all of the major morphological characteristics, the one feature which does not conform with the proposed life position is the angle of the articular facet. According to the benthic theory the arms lay horizontally on the substrate perpendicular to the axis of the calyx. However, as the radial facet is situated in the upper margin of the radial, perpendicular to the radial ridge, the articulation with the first brachial is directed vertically rather than horizontally. Therefore it is proposed that there was a slight proximal arching of the arms which prevented the oral surface from sinking below the sediment/water interface.

#### THE PRESENCE OF *SACCOCOMA* IN THE SOLNHOFEN LIMESTONE

The abundance of *Saccocoma* in the Solnhofen Limestone remains an enigma. It is possible that as they were unattached and free living they were easily picked up by currents and washed into the basin. The influx of water into the basin would disrupt the salinity stratification, which is considered the reason for the absence of a typical benthos (Seilacher 1963; Barthel 1964; Goldring and Seilacher 1971; Keupp 1977), and for a time it is possible that productivity extended from the basin floor to the water surface. Thus the saccocomids may represent opportunists exploiting a normally hostile environment.

Many of the distinguishing morphological features of saccocomids can be interpreted as adaptations to the basin environment. It has been postulated (Hemleben 1977) that the colonization of the Solnhofen basin by macrobenthos was inhibited by the soupy texture of the sediment surface. The wing-like flanges which occur on the proximal brachials of saccocomids would have supported them on the sea floor. Similar adaptations are seen in the rare examples of accepted benthic animals which occur in the Solnhofen Limestone. The gastropod *Spinigera spinosa* has two long spines, developed on each whorl perpendicular to the longitudinal axis, which have been interpreted as soft sediment supports (Viohl 1985).

In the quiet stable environment of the plattenkalk basins, the collecting-bowl feeding posture would have been ideal. The arms were able to arch upwards away from the sediment surface and thus avoid contact with the substratum and contamination by detrital sediment. The abundance of coccoliths and other protists would provide a suitable diet, similar to that recorded for the suspension-feeding brittlestar *Ophiothrix fragilis* (Warner and Woodley 1975).

It is possible that saccocomids could survive in the plattenkalk basins only for short periods of time. However, no crawling traces attributable to *Saccocoma* are recorded from the Solnhofen Limestone. If the crinoids were killed by sudden influxes of sediment it is possible that only the tracks of animals mobile at the time of burial would be preserved. It is also plausible that the surface prohibited crawling. If the sediment was poorly consolidated it is likely that the saccocomids were unable to crawl and rather than being free living they tended to stay in the same location.

#### CONCLUSIONS

Based on morphological evidence, the mode of life of *Saccocoma* was benthic. Functional morphological interpretation leads to the conclusion that *Saccocoma* lay passively on the basin floor with the calyx embedded in the soft sediment. The flanges on the brachials probably acted as supports. At approximately mid-length the arms arched upwards. The distal ramules formed an effective multidirectional feeding baffle which could intercept currents from any direction and/or feed on gravitationally settling food particles.

The primary mode of locomotion in *Saccocoma* was probably crawling. However, the poorly consolidated sediment in the plattenkalk basins inhibited movement. *Saccocoma* was also able to swim but this facility was probably only utilized as an escape mechanism.

The sheer numbers of *Saccocoma* in the Solnhofen Limestone suggest that it was an opportunist. It was brought into the basin during periods of oceanic exchange which caused total mixing of the

basin waters and destroyed the salinity stratification. Not all the specimens brought into the basin survived but those that did flourished on the basin floor undisturbed. Populations were ultimately killed by sudden influxes of sediment which buried the saccocomids and preserved them fully articulated.

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